# Northumbria Research Link

Citation: Guy, Travis J., Hutchinson, Matthew C., Baldock, Katherine, Kayser, Elisha, Baiser, Benjamin, Staniczenko, Phillip P.A., Goheen, Jacob R., Pringle, Robert M. and Palmer, Todd M. (2021) Large herbivores transform plant-pollinator networks in an African savanna. Current Biology, 31 (13). 2964-2971.e5. ISSN 0960-9822

Published by: Elsevier

URL: https://doi.org/10.1016/j.cub.2021.04.051 <https://doi.org/10.1016/j.cub.2021.04.051>

This version was downloaded from Northumbria Research Link: http://nrl.northumbria.ac.uk/id/eprint/46193/

Northumbria University has developed Northumbria Research Link (NRL) to enable users to access the University’s research output. Copyright © and moral rights for items on NRL are retained by the individual author(s) and/or other copyright owners. Single copies of full items can be reproduced, displayed or performed, and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided the authors, title and full bibliographic details are given, as well as a hyperlink and/or URL to the original metadata page. The content must not be changed in any way. Full items must not be sold commercially in any format or medium without formal permission of the copyright holder. The full policy is available online: http://nrl.northumbria.ac.uk/policies.html

This document may differ from the final, published version of the research and has been made available online in accordance with publisher policies. To read and/or cite from the published version of the research, please visit the publisher’s website (a subscription may be required.)

Northumbria University NEWCASTLE

CUSTOMER SERVICE EXCELLENCE CSE UniversityLibrary

# Title: Large herbivores transform plant-pollinator networks in an African savanna

**Authors:** Travis J. Guy[1,2,9], Matthew C. Hutchinson[3,9], Katherine C. R. Baldock[2,4,5], Elisha Kayser[2], Benjamin Baiser[6], Phillip P. A. Staniczenko[7], Jacob R. Goheen[2,8], Robert M. Pringle[2,3], & Todd M. Palmer[1,2]*

**Affiliations:**

[1] Department of Biology, University of Florida, Gainesville, FL 32611, USA.

[2] Mpala Research Centre, Laikipia, Kenya.

[3] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA.

[4] School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK.

[5] Department of Geographical and Environmental Sciences, Northumbria University, Newcastle upon Tyne NE1 8ST, UK

[6] Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32603, USA.

[7] Department of Biology, Brooklyn College, City University of New York, NY 11210, USA.

[8] Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.

**Author list footnotes:**

[9] These authors contributed equally.

* Corresponding author and Lead Contact

**Corresponding author and Lead Contact e-mail address**: tmp@ufl.edu

## Summary

Pollination by animals is a key ecosystem service[1,2] and interactions between plants and their pollinators are a model system for studying ecological networks[3,4], yet plant-pollinator networks are typically studied in isolation from the broader ecosystems in which they are embedded. The plants visited by pollinators also interact with other consumer guilds that eat stems, leaves, fruits, or seeds. One such guild, large mammalian herbivores, are well-known ecosystem engineers[5–7] and may have substantial impacts on plant-pollinator networks. Although moderate herbivory can sometimes promote plant diversity[8], potentially benefiting pollinators, large herbivores might alternatively reduce resource availability for pollinators by consuming flowers[9], reducing plant density[10], and promoting somatic regrowth over reproduction[11]. The direction and magnitude of such effects may hinge on abiotic context—in particular, rainfall, which modulates the effects of ungulates on vegetation[12]. Using a long-term, large-scale experiment replicated across a rainfall gradient in central Kenya, we show that a diverse assemblage of native large herbivores, ranging from 5-kg antelopes to 4000-kg African elephants, limited resource availability for pollinators by reducing flower abundance and diversity; this in turn resulted in fewer pollinator visits and lower pollinator diversity. Exclusion of large herbivores increased floral-resource abundance and pollinator-assemblage diversity, rendering plant-pollinator networks larger, more functionally redundant, and less vulnerable to pollinator extinction. Our results show that species extrinsic to plant-pollinator interactions can indirectly and strongly alter network structure. Forecasting the effects of environmental change on pollination services and interaction webs more broadly will require accounting for the effects of extrinsic keystone species.

## Results

Human transformation of the biosphere threatens animal pollination services and has motivated theoretical and empirical research seeking to identify generalities in the structure of mutualistic networks between plants and their pollinators[13]. Considerable effort has been invested in predicting how, for example, network structure and functioning will change as native plant and pollinator species are lost[14–18] or as novel species invade[19,20]. However, several uncertainties cloud our understanding. One is the role of ‘extrinsic’ species in shaping ecological networks. Plants and pollinators are embedded within complex communities, and species that do not participate in pollination interactions may nonetheless exert strong effects on plant-pollinator networks[19,21,22]. Similarly, network structure and stability—and their alteration by extrinsic species—may vary across environmental gradients in ways that are difficult to predict but essential to understand[23].

Large mammalian herbivores are one guild of extrinsic keystone species[24] likely to influence the structure and emergent properties of plant-pollinator networks. Grazing, trampling, and nutrient redistribution by large herbivores—and the cessation of these activities when populations crash—alter vegetation structure[5,6,25] and composition[26,27], and indirectly affect animals[7,28]. Global large-herbivore declines[29,30] therefore have the potential to reorganize ecological networks, but this possibility has not been assessed. On the one hand, moderate grazing pressure can elevate plant diversity (e.g., by suppressing dominant competitors[8]), which might foster larger, more stable plant-pollinator networks—consistent with the intermediate-disturbance[31] and keystone-consumer hypotheses[32] and with theories predicting a positive relationship between complexity and stability in mutualistic networks[33]. On the other hand, large herbivores eat flowers[9], reduce plant density through trampling and consumption[10], and prompt plants to reallocate energy to growth in lieu of reproduction[11]; these effects might reduce resource availability for pollinators and generate smaller, more fragile plant-pollinator networks. Importantly, rainfall mediates the effects of herbivory on vegetation[12] and may therefore also mediate large herbivore impacts on plant-pollinator networks. Evidence from pastoral[34,35] and ungulate-invaded landscapes[21,36] suggests that plant-pollinator interactions are suppressed by large herbivores but we have little understanding of how these interactions are affected by species-rich assemblages of native herbivores.

We experimentally tested how native large herbivores affect plant-pollinator networks in a semi-arid African savanna ecosystem (Mpala Conservancy, Kenya) with a diverse community of large herbivores, plants, and pollinators. The large-herbivore assemblage comprises ~24 species spanning three orders of magnitude in body size from dik-dik (*Madoqua* cf. *guentheri*, 5 kg) to African elephants (*Loxodonta africana*, 4000 kg). The biomass density of native large herbivores at Mpala is roughly 5000 kg km$^{-2}$ [37], which is typical of semi-arid African savannas[38]. Rainfall varies across the conservancy, with ~30% more precipitation on average in the south than the north (2009-2014, mean annual rainfall ± SEM: south, 595 ± 64 mm; north, 493 ± 69 mm). We quantified the effects of large herbivores on plant-pollinator networks, and the role of rainfall in modulating these interactions, using the UHURU experiment[10]. This series of fenced 1-ha herbivore exclosures and unfenced control plots was established in 2008 and is replicated in blocks from south (wetter) to north (drier; Figure S1A-C). Six years into the experiment (June 2014, an annual flowering peak; Figure S1D-E), we recorded plant-pollinator interactions in three total exclosures (which exclude all herbivores ≥ 5 kg, hereafter 'Exclusion' plots) and paired control ('Open') plots in both the northern and southern sites (12 total plots). Within each plot (specifically the central 0.25-ha subplot), we measured floral abundance, caught and identified flower-visiting insects (hereafter 'pollinators'), and used these data to estimate plant-pollinator networks.

Large-herbivore exclusion increased plot-level richness and abundance of floral resources (Figure 1A-B; see *Methods*). In total, we recorded flowers from 71 plant species in the six Exclusion plots compared with only 51 in Open plots. On average, Exclusion plots had 50% more flowering plant species and threefold more floral units (individual flowers or composite inflorescences) per plant species than did Open plots (Figure 1A-B). Neither floral richness nor floral abundance differed between high- and low-rainfall sites; however, a site-by-treatment interaction indicated that the reduction of floral richness by herbivores was greater in the low-rainfall site (Figure 1A). Of the 39 species widespread enough to estimate an experimental effect (*Methods*), almost all of them (36 of 39; 92%) had higher mean floral abundance in Exclusion plots (fourfold higher on average; Figure S2A).

Pollinator activity was greater and assemblages were larger in Exclusion plots (Figure 1C-E). We captured 1,819 individual pollinators representing 331 insect species or morphospecies from 59 families (Table S1) during floral-visitation surveys (*Methods*). Coverage-based rarefaction[39] indicated that Exclusion plots had roughly 50% more pollinator species and 50% greater pollinator diversity (Hill's numbers, $q$ = 1) than Open plots (Figure 1C,E). In addition, pollinators were more active in Exclusion plots (Figure 1D), where we observed nearly 20% more flower visits per hour of sampling. Pollinator-assemblage composition varied widely among plots and was significantly correlated with floral-assemblage composition (Mantel test, compositional dissimilarity of pollinators and flowers: $r = 0.69$, $P < 0.001$). Moreover, partial distance-based redundancy analysis (conditioned on sampling effort) showed that pollinator-assemblage composition (presence/absence) differed between rainfall levels (sites) and, to a lesser extent, between herbivore-exclusion treatments (Figures 2A & S3). Pollinator assemblages were least similar among Open plots due to turnover in species composition (Figure S3). Pollinator-assemblage dissimilarity due to species loss was greatest for Open-Exclusion comparisons and at the low-rainfall site (Figure S3), suggesting that pollinator species differed in their likelihood of co-occurring with large herbivores. A subset of pollinators were consistently caught at a higher rate in Exclusion plots (Figure 2B, at right); three bee genera (*Apis*, *Hypotrigona*, *Pseudapis*) were the greatest beneficiaries of herbivore exclusion. Species captured at higher rates in Open plots (Figure 2B, at left) comprised a mixture of guilds including a few bee taxa (e.g., *Patellapis*, *Liotrigona*, *Amegilla*) as well as primarily carnivorous and detritivorous flies (e.g., *Neolophonotus*, *Musca*, *Physiphora*). All pollinators are shown in Figure S2B.

Exclusion of large herbivores exerted strong effects on network structure, whereas the effect of rainfall was typically smaller (Figures 3A-F; *Methods*; Table S2). In Exclusion plots, plant species were visited by 60% more pollinator species (Figure 3B) and received 2.6-fold more pollinator visits (Figure 3C). Plant-pollinator networks were not more nested in Exclusion plots (Figure 3D), but they were substantially less specialized (Figure 3E), potentially indicating greater redundancy of plant-pollinator interactions when large herbivores were absent. Lower visitation intensity and interaction redundancy in Open plots might have been balanced by greater pollinator specialization, but we found no evidence for this hypothesis (Figure 3F). The effect of large herbivores on network structure was greatly reduced when we statistically accounted for floral and pollinator richness as well as interaction intensity (Table S2), indicating that large herbivores altered network structure through their effects on the richness and density of flowers and pollinators.

Lower diversity, intensity, and redundancy of plant-pollinator interactions in Open plots may render these networks more vulnerable to species loss. To assess vulnerability, we used a Bayesian network approach (*sensu*[40,41]; *Methods*) to calculate the average number of pollinators lost from each network across all possible extinction sequences. We parameterized the Bayesian network with a baseline extinction probability for each species (i.e., pollinators observed rarely were attributed a greater extinction risk) that increased linearly as interaction partners were lost (*Methods*). A greater proportion of pollinators were predicted to be lost at the low-rainfall site (North) and in the Open plots within each site (Figure 3G). When we statistically accounted for plant and pollinator richness as well as interaction intensity (*Methods*), rainfall (site) remained a strong predictor of pollinator loss, whereas the effect of herbivory treatment was greatly reduced (Table S2). As for network-structure metrics, large herbivores affected pollinator vulnerability via their suppression of floral and pollinator richness and density.

## Discussion

Mutualistic networks, such as those comprising plants and pollinators, are regarded as the "architecture of biodiversity"[3]; however, they are generally studied in isolation from their broader community context. Our experimental results show that large mammalian herbivores suppress the richness and density of flowers and pollinators, leading to more fragile plant-pollinator networks. These effects were most pronounced at our low-rainfall site[7,42] suggesting that shifting rainfall patterns[43] and declining wildlife populations[44,45] in East Africa may interact to affect pollination services.

Our results suggest a tension between pollination and large-mammal herbivory in intact African savannas, and a key question is whether the same effects would be evident if large herbivores were excluded for longer durations or extirpated from entire landscapes. In our plots, herbivore exclusion has increased vegetation cover and large-tree density, altered understory composition in favor of animal-pollinated forbs and subshrubs relative to wind-pollinated grasses, and increased plant reproductive output[26,46], all of which helps explain effects on floral resources and pollinators[47]. Long-term, ecosystem-level declines in herbivore populations precipitate similar effects on vegetation structure[5,6,25,48]. In principle, large-herbivore collapse could trigger regime shifts from savanna to closed-canopy woodland, although this hinges on various environmental factors (notably rainfall and fire). In another experiment at our semi-arid site, where fires are infrequent, woody canopy cover plateaued at roughly 60% after 17 years of herbivore exclusion[49], suggesting that a regime shift is unlikely. In wetter savannas with higher, more contiguous understory biomass, successional shifts are more likely, but so too is the likelihood that herbivore loss leads to more frequent, intense fires[50,51] that arrest succession and may suppress plant-pollinator interactions[52–54].

We hypothesize that the suppression of pollinator (alpha) diversity documented here may be partially offset at large spatial scales by herbivores' maintenance of vegetation heterogeneity, which should tend to enhance pollinator beta and gamma diversity. Herbivores maintain vegetation heterogeneity via selective consumption of vegetation[55,56], water- and risk-sensitive space use[57–59], and nutrient redistribution[60], all of which produce patchy mosaics of plant biomass and species composition. By contrast, extreme alternative outcomes of wholesale herbivore extirpation—succession resulting in canopy closure or intense, grassland-promoting fire regimes—would have homogenizing effects on plant communities and, by extension, pollinators. Large herbivores suppress plant-pollinator interactions but understanding the scale-dependence of this effect is important; to that end, studies are needed that complement our mechanistic experimental approach by evaluating large-herbivore effects on plant-pollinator networks across a gradient of ecosystems with varying ungulate biomass density, rainfall, and fire regimes.

Discerning links from lions and leopards to bees and butterflies, mediated by herbivores, plants, and abiotic variables in savannas will provide a more complete picture of pollination in savannas. In doing so, it may be necessary to conceptualize all primary consumers—from ungulate herbivores and pollinating bees to granivorous rodents and frugivorous birds—as competitors for the same plant-derived nutrition. In the light of resource competition, the negative impacts of ungulates on pollinators are more intuitive. Yet our finding that plant-pollinator networks are more robust (at least locally) in the absence of native large herbivores poses something of a riddle: Why does a natural component of an ecosystem (large herbivores) appear to destabilize another natural component of the same system (plant-pollinator interactions)? Scale-dependence might provide one answer to this question. Another answer might be that projecting 'stability' or related properties from bipartite networks, in the absence of contextualizing information on their biotic and abiotic context, is likely to be misleading. Our findings underscore the value of considering extrinsic species in bipartite-network analyses; future studies may need to go even further in situating network analyses in their broader ecological context if the aim is to produce useful forecasts of network dynamics and ecosystem services in a rapidly changing world.

## Acknowledgements

We acknowledge field technicians Zachary Ntanyaki, Julius Nankini, and Peter Ekai, and the taxonomists listed in Table S1. Patrick Milligan and Kristen Prior provided technical assistance. J. C. Ruiz-Guajardo and Gavin Ballantyne assisted in field sampling and insect cataloging. T.J.G. was supported by a Tropical Conservation and Development Research Grant from the University of Florida, a Sigma Xi Grant-in-Aid of Research, and NSF Research Fellowship DGE-1315138. M.C.H. and R.M.P. acknowledge support from the High Meadows Environmental Institute and Department of Ecology and Evolutionary Biology at Princeton University. Research was supported by NSF grants DEB-1556905 and DEB-0827610 (T.M.P.), DEB-1930763 and DEB-1547679 (J.R.G.), and IOS-1656527 (R.M.P.), and by NERC grant NE/M006956/1 (K.C.R.B.).

## Author Contributions

T.J.G., K.C.R.B., and T.M.P. conceptualized the study; T.J.G., K.C.R.B., E.K., and T.M.P. developed and implemented the methodology; T.J.G., M.C.H., B.B., and P.P.A.S. contributed software and formal analyses; K.C.R.B., J.R.G., R.M.P., and T.M.P. contributed resources, funding, and project administration; M.C.H. visualized the data; K.C.R.B., R.M.P., and T.M.P. supervised the first authors; T.J.G., M.C.H., K.C.R.B. and T.M.P. prepared the original draft; all authors contributed to draft review and editing.

## Declaration of Interests

The authors declare no competing interests.

## Figure titles and legends

**Figure 1. Large-herbivore exclusion increased plant and pollinator richness and density.** Floral species richness (A; treatment: $\chi^2 = 5.64$, df = 1, $P = 0.02$) and the number of flowers per plant species (B; treatment: $\chi^2 = 9.68$, df = 1, $P = 0.002$) were greater in Exclusion plots than in Open plots. Although there was no effect of rainfall site on either of these responses (site: $\chi^2 = 0.98$, df = 1, $P = 0.32$ and $\chi^2 = 2.40$, df = 1, $P = 0.12$, respectively), rainfall appeared to modulate the effect of herbivores on floral species richness (A; site×treatment: $\chi^2 = 3.10$, df = 1, $P = 0.08$). Rarefied pollinator species richness (C; treatment: $\chi^2 = 5.10$, df = 1, $P = 0.02$), number of pollinator individuals captured (D; treatment: $\chi^2 = 3.94$, df = 1, $P = 0.05$), and rarefied pollinator diversity (E; treatment: $\chi^2 = 4.51$, df = 1, $P = 0.03$) were all greater in Exclusion plots but did not differ between sites (site: $\chi^2 = 0.49$, df = 1, $P = 0.48$, $\chi^2 = 0.02$, df = 1, $P = 0.88$, and $\chi^2 = 2.03$, df = 1, $P = 0.15$, respectively). All reported effects are likelihood-ratio tests, bars and error bars show mean ± 1 SEM per treatment-site combination ($n = 3$). See also Figure S2 and Table S2.

**Figure 2. Large herbivores and rainfall reorganized pollinator assemblages**. (A) Partial distance-based redundancy analysis (conditioned on sampling effort) separated pollinator assemblages by site (horizontal axis explaining 14% of variance; low-rainfall plots have negative values, high-rainfall plots have positive values) and treatment (vertical axis explaining 11% of variance; Open plots have negative values, Exclusion plots generally have positive values). Rainfall most strongly modulated pollinator assemblages and herbivore presence had a smaller effect (permutational ANOVA, n = 9999, adjusted $R^2 = 0.06$; site, $F_{1,8} = 1.48$, $P = 0.002$; treatment, $F_{1,8} = 1.17$, $P = 0.14$). See also Figure S3. (B) Response to herbivore exclusion for the most widespread pollinator species (those present in both plots of at least two experimental blocks), quantified as the log-response ratio of each species' change in capture rate between Exclusion and Open plots (mean ± 1 SEM). Species captured at higher rates in Exclusion plots tended to be those that specialize on nectar and pollen (at right; *Apis, Hypotrigona, Pseudapis*), whereas species captured at lower rates in Exclusion plots (at left) were more trophically diverse, comprising both nectar and pollen specialists (*Patellapis, Liotrigona* bees) and other guilds (e.g.,

predatory *Neolophonotus* flies, detritivorous *Musca* and *Physiphora* flies). Points and error bars are mean ± 1 SEM. See also Figure S2 and Table S2.

**Figure 3. Large-herbivore exclusion made plant-pollinator networks larger, more generalized, and less vulnerable to pollinator loss.** Bipartite networks (A) show the plot-level plant-pollinator networks where large herbivores were present (at left) and excluded (at right). In Exclusion plots, plants were visited by more pollinator species (B; treatment: $\chi^2 = 9.31$, df = 1, $P = 0.002$; site: $\chi^2 = 3.47$, df = 1, $P = 0.06$) and were visited more frequently (C; treatment: $\chi^2 = 5.66$, df = 1, $P = 0.02$; site: $\chi^2 = 0.56$, df = 1, $P = 0.46$). In Exclusion plots, plant-pollinator networks were not more nested (D; treatment: $\chi^2 = 1.34$, df = 1, $P = 0.25$; site: $\chi^2 = 0.03$, df = 1, $P = 0.87$), but they were less specialized (E; treatment: $\chi^2 = 4.43$, df = 1, $P = 0.04$; site: $\chi^2 = 0.90$, df = 1, $P = 0.34$). Lower overall visitation rates and interaction redundancy in Open plots were not mitigated by increased pollinator specialization (F; treatment: $\chi^2 = 0.69$, df = 1, $P = 0.41$; site: $\chi^2 = 1.20$, df = 1, $P = 0.27$). Plant-pollinator assemblages were less vulnerable to pollinator extinction in Exclusion plots and at the wetter site, where a smaller proportion of the pollinator assemblage was predicted to be lost due to low abundance and specialized interaction patterns (G; treatment: $\chi^2 = 3.60$, df = 1, $P = 0.06$; site: $\chi^2 = 7.35$, df = 1, $P = 0.01$). All reported effects are likelihood-ratio tests, bars and error bars show mean ± 1 SEM per treatment-site combination ($n = 3$). See also Table S2.

## STAR Methods

### Resource Availability

***Lead Contact:*** Further information and requests should be directed to and will be fulfilled by the Lead Contact, Todd M. Palmer (tmp@ufl.edu).

***Materials Availability:*** All specimens are stored in the institutional collections of the entomologists listed in Table S1 and will be made available by the Lead Contact upon reasonable request.

***Data and Code Availability:*** The datasets that support these findings are provided on Dryad: https://doi.org/10.5061/dryad.bcc2fqzc1. Data provided tabulate floral and pollinator surveys as well as plot-level plant-pollinator networks. All code used in data analysis is freely available in the R programming language and open-source packages therein.

### Experimental Model and Subject Details

***Study Site*****:** Our experiment was conducted within the Ungulate Herbivory Under Rainfall Uncertainty ("UHURU") experiment at Mpala Conservancy in Laikipia County in central Kenya (0°17'N, 37°52'E). Mpala is located at an elevation of approximately 1600m and is home to a diverse wildlife community[10]. The UHURU experiment was established in September 2008 and consists of replicated 1 ha (100 m x 100 m) herbivore exclosures established at three sites along a 20-km rainfall gradient, which range from an average of ~490 mm of rain per year in the northern, low rainfall area to an average of ~600 mm per year in the southern, higher rainfall area. Each of the three sites comprises three blocks, and each block contains four 100 m x 100 m plots randomly assigned to each of four herbivory treatments (Figure S1A-C).

***Experimental Setup*****:** The four herbivory treatments are "total" exclusion, "meso-herbivore" exclusion, "mega-herbivore" exclusion, and open control (Figure S1C). In this study, we used only the total-exclusion and open control plots from each block. The former exclude all herbivores larger than 5 kg mass and ~50 cm height, (but not hares and other small mammals) using 2.4-m high fences comprising 14 strands of electrified wire with a 1 m high chain-link barrier (10 cm mesh) at ground level. Open plots are unfenced, with a series of 1-m tall wooden posts at 10 m intervals demarcating plot boundaries and allowing complete access to all herbivores.

In this study, we evaluated plant-pollinator assemblages at the North and South sites. These sites are similar in soil properties, but differ in historical patterns of average annual rainfall, with the North site typically receiving less rainfall than the South (mean annual rainfall ± SE: 493 mm ± 69 vs. 595 mm ± 64, for North and South 2009-2014, respectively), and having lower understory vegetative diversity and richness[10].

The UHURU experimental design allowed us to test the effects of excluding large-mammalian herbivores on floral abundance, pollinator activity, and plant-pollinator interaction networks, and to assess whether these effects are modulated by aridity. We note that the UHURU experiment does not simulate the elimination of herbivores at the landscape level; rather, it simulates the loss of large-mammalian herbivores from hectare-scale patches within the landscape. Thus, for highly mobile pollinator species, large-herbivore exclusion at the spatial scale of our experiments is likely to influence the patchiness of the landscapes they forage across and the habitat that they select; nonetheless, we expect this experimental scenario to be a reasonable proxy for the likely effects of large mammal defaunation on plant and pollinator assemblages[28].

## Method Details

***Survey Approach*:** Data for plant-pollinator visitation networks were collected from May 30 to July 3 2014 at the end of the long rains when flowering is most common (Figure S1D-E). Within 12 plots from the UHURU experiment (2 treatments x 3 replicates x 2 sites), we collected data on plant-pollinator interactions by catching and identifying all flower-visiting insect taxa (hereafter "pollinators") in a central 50m x 50m (0.25 ha) subplot of each experimental plot. To facilitate these surveys, each subplot was further divided up into 25 quadrats (10m x 10m) to ensure that no flower was missed. For simplicity, we refer to the data collected within each plot's central 0.25 ha subplot as representing the entire plot. We sampled both floral abundance and pollinator visits in the Exclusion plot and Open plot of a given block before proceeding to the next block. For each block, we undertook both floral and pollinator visitation surveys at the Exclusion plot first before moving to the Open plot. We randomly assigned the order in which each block would be sampled at each site and alternated sampling between South and North sites.

***Floral Surveys*****:** In the central subplot (0.25 ha) of each experimental plot, we conducted floral abundance surveys during the morning of the day preceding pollinator visitation sampling. Each floral survey was repeated the same afternoon to account for any afternoon-blooming plants that would have been missed during the morning survey. We recorded the total number of floral units (defined as an individual flower or composite inflorescence in the case of composite flowers) for each flowering plant species within the central subplot. Floral abundance was expressed as the total number of open floral units in each subplot. In this study, flowering-species richness indicates the number of plant species with open flowers in the sampling area (i.e., species density[61]). Plant species were identified using keys and descriptions in[62] and taxonomically verified specimens in the local UHURU herbarium[63]. Of the 76 plant species that were flowering during our surveys, 95% (72/76) were identified to species with a further two being identified to genus.

***Pollinator Surveys*****:** The day after a plot's floral survey, we sampled insect visitors at every flowering species recorded to have 10 or more floral units in the central 0.25 ha subplot during the previous day's floral survey. Each qualifying flowering species was observed for 30 minutes during each of three time periods (0800-1030; 1030-1300; 1330-1600, for 90 minutes total observation time), which spanned the most active time for pollinators[64]. If a species' flowers were not open during a specific time period, it was not given additional time in another time period. When more flowering species were blooming in a plot than was possible to watch in one day, two subsequent days following the floral survey were used and species were randomly assigned a day to be observed. Weather data were not quantitatively tracked, however we did note weather conditions during each survey and these were qualitatively consistent across sites and treatments (i.e., generally sunny with occasional cloudiness or breeze). In the two instances of unfavorable weather (persistently cloudy and windy), we postponed flower-visitor observations by one day.

For each flowering species at each time period, we randomly chose a 1 $m^2$ area for observation that contained at least 10 floral units. If less than 10 floral units for a given plant species occurred in a 1$m^2$ area, the location to be watched was chosen based on the watchable area with the highest concentration of floral units (e.g., an area with 7 open flowers given preference over an area with 3 open flowers). Observers stood at a distance of ~1 m to minimize disturbance to visiting insects. Any insect touching a reproductive part of the plant was captured (89% success rate). Captured insects were euthanized in kill jars using ethyl acetate, pinned, dried, and then identified to species or genus and morphospecies by 27 taxonomic experts across the globe familiar with African insects (Table S1). Escaped insects were noted and identified by eye to the lowest taxonomic resolution possible but were excluded from our analyses to avoid potential biases in identification. Ants (Formicidae) were excluded from our analyses because they are rarely effective pollinators and can depress seed set[65]. In total, our dataset was composed of 1819 captured flower visitors.

## Quantification and Statistical Analyses

***Data Quality Control*:** All analyses were conducted in R[66]. Prior to analysis, we conducted several quality-control steps on the data. To compare floral abundance among plots, we computed the number of flowers per flowering-plant species in each plot to control for among-plot differences in flowering-species richness. Next, we corrected the pollinator richness of our insect collections to account for differing total sampling time between plots. To make pollinator richness comparable among plots, we used coverage-based rarefaction and extrapolation[39,67] with the R package *iNEXT* v2.0.20[68] to estimate pollinator richness at the maximum sampling completeness among all plots (70.4% sample coverage; determined as the smallest sampling completeness after each plot's sample size is doubled, as per[39]). Using the same method, we also estimated the Shannon diversity of the pollinator assemblage (Hill's numbers, q = 1,[68]). Estimating pollinator richness and diversity at equal levels of sampling completeness facilitated direct comparisons between plots[39]. To compare the number of pollinator individuals caught in each plot, we included effects of per-plot sampling effort in statistical analyses. Sampling effort was calculated as the number of 'flower hours' of sampling in each plot (i.e., number of floral units observed multiplied by total sampling time). Given the low replication per treatment-site combination in this large-scale experiment and our statistically conservative use of plots as the units of analysis, we considered $P \leq 0.10$ as grounds for biological inference to balance the potential for type I and type II errors.

***Floral and Pollinator Assemblage Analyses*:** To determine how the floral and pollinator assemblages differed between Exclusion and Open plots, and to assess the potential rainfall-site dependence of these effects, we constructed generalized linear mixed models (GLMMs) with by-block random intercepts using the R package *glmmTMB* (*v*1.0.1,[69]). For each metric, we constructed four candidate models that included experimental block (i.e., paired Exclusion and Open plots) nested within site (North or South) as a random effect and fixed effects of herbivore presence, site, both, and both plus the interaction term (see Table S2). For models of caught pollinators, we also included sampling effort (flower hours; log) as a fixed effect in each candidate model. Because species richness and abundance are recorded as counts, we used the generalized Poisson error distribution with a log link function for flowering-species richness (Figure 1A) and caught pollinators (Figure 1D). For flowers-per-plant-species (Figure 1B), rarefied pollinator richness (Figure 1C), and rarefied pollinator diversity (Figure 1E), we used a Gaussian error distribution because these measures are continuous, positive variables. We log-transformed flowers-per-plant-species to meet model assumptions. We performed residual diagnostics (including checks for heteroskedasticity and dispersion) for each candidate model using the *DHARMa* package (v0.3.2[70]) and tested for overdispersion in Poisson-family models using the *performance* package (v0.4.7[71]) in R. To assess how herbivore presence and rainfall site influenced the species richness, density, and diversity of flowers and flower-visitors, we compared candidate models with and without each predictor variable using one-sided likelihood-ratio tests with the *anova* function in R.

We also evaluated the impact of herbivore exclusion on particular plant and pollinator species. For each experimental block (paired Exclusion and Open plots), we identified the floral and pollinator species that were observed in both plots within each block. For these species, we calculated the log-response ratio [log-response ratio; ln(Exclusion/Open)] to quantify the effect of herbivore exclusion on their abundance[7]. For plant species (Figure S2A), we used their number of floral units per plot as a measure of each species' abundance. For pollinator species (Figures 2B & S2B), we used each species' capture rate as the measure of abundance. Using capture rate for pollinators (number caught per flower-hour of observation) meant that our estimates of pollinator species' abundance controlled for differing sampling effort per plot. A disadvantage of this approach was that, because assemblages differed in diversity, the probability of capturing any one species was lower in higher diversity plots. Because Exclusion plots had more diverse pollinator assemblages, pollinator capture rate therefore represents a conservative measure of pollinator abundance for the species that respond positively to herbivore exclusion. For all plants and pollinators appearing in both plots of at least two experimental blocks, we calculated the mean and standard error of the mean to estimate the overall response to the experiment for each species and identify plants and pollinators that benefit (positive log-response ratio) and suffer (negative log-response ratio) from herbivore exclusion.

***Pollinator Assemblage Dissimilarity*:** To assess the similarity of pollinator-assemblage membership, we calculated pairwise Jaccard dissimilarities between plots using the *betapart* package (v1.5.1[72]). We used a presence-absence dissimilarity metric to focus our assessment on community membership and the Jaccard indices specifically due to their robustness to undersampling[73]. We computed three components of compositional dissimilarity: total dissimilarity (measured as Jaccard dissimilarity, $\beta_{JAC}$), dissimilarity resulting from species turnover (measured as the turnover fraction of Jaccard dissimilarity, $\beta_{JTU}$), and dissimilarity resulting from nestedness (measured as nestedness-resultant fraction of Jaccard dissimilarity, $\beta_{JNE}$). Before analyzing the dissimilarity of pollinator assemblages, we examined the data for spatial structure with distance-based Moran's Eigenvector Maps (implemented with the *quickMEM* function, v1.0.0, provided in *Numerical Ecology with R* pp.327[74] and adjusted for distance-based RDA). The latitude and longitude of each plot's centroid were used to represent the geographic location of each plot. If significant spatial structure existed in the data, spatial eigenvectors could be used to condition partial-redundancy analysis of compositional dissimilarity. However, no significant spatial structure was found across the pollinator assemblages of the 12 plots ($\beta_{JAC}$, $P = 1.00$; $\beta_{JTU}$, $P = 1.00$; $\beta_{JNE}$, $P = 0.99$). As such, we did not include spatial variables in downstream analyses of compositional dissimilarity. To explore the connection between floral and pollinator assemblage composition, we tested for a correlation between total pollinator dissimilarity ($\beta_{JAC}$) and the same for plot-level floral assemblages using the *mantel* function in *vegan* (v2.5.6[75]), comparing the observed Mantel statistic to 9999 permuted values of the statistic. Next, to explore how site and herbivore presence influenced each component of pollinator dissimilarity (i.e., $\beta_{JAC}$, $\beta_{JTU}$, $\beta_{JNE}$ from above), we used partial distance-based redundancy analysis (dbRDA; implemented with *capscale* in *vegan*, v2.5.6[75]). Partial dbRDA was conditioned on plot-level sampling effort (as estimated using the 'flower hours' of sampling per plot) to control for differences in pollinator sampling between plots (Figures 2A & S3). For each of the three dissimilarity partitions, we computed a partial dbRDA with additive constraints of herbivore treatment and site, assessed model fit with adjusted $R^2$, and quantified the importance of treatment and site for the clustering of plots with permutational ANOVA (9999 permutations). The effect of treatment and site individually were derived by comparing one model containing each variable only to the additive model containing both treatment and site.

***Plant-Pollinator Network Construction*:** Flower visitation surveys for each plant species were carried out in the position of each sampling area (central 50 x 50 m subplot within each experimental plot) where the greatest number of flowers could be closely observed. As a result, we were not able to conduct visitation surveys for all of the flowers belonging to each species. To produce a complete characterization of the plant-pollinator networks within each sampling area, we scaled up the set of observed flower visitation events to the entire 0.25ha subplot. Specifically, we estimated the expected number of visitation events between each plant and pollinator in each subplot (hereafter, interaction intensity) as the number of observed visitation events divided by the proportion of that plant species' flowers within the subplot that were observed during visitation surveys (Figure 3A). For example, if pollinator *a* was observed to visit plant *b* three times and 10 of *b*'s flowers were observed out of 40 flowers within the plot, the interaction $i_{a,b}$ was taken to be 3/0.25 (i.e., 12). Scaling plant-pollinator interactions in this way enabled us to account for each plant species' total floral abundance while dedicating equal sampling effort to each plant species.

***Plant-Pollinator Network Structure Analyses*****:** To describe the topology of plant-pollinator interaction networks, we calculated a set of species- and network-level metrics that capture plant-pollinator interaction patterns and have direct ecological interpretations. First, at the plant-species level, we computed the number of pollinator species observed to visit each plant species in each plot as well as each plant species' visitation intensity—the total number of scaled pollinator visits per plant species. Together these metrics capture the potential for redundancy in pollination services and the potential for pollination provisioning. For each pollinator species in each plot, we calculated their specialization in resource use with the *d'* metric (measured in R with the *specieslevel* function in *bipartite* v2.15[76,77]), which estimates each species' deviation from random resource use. At the whole-network scale, we computed metrics that describe the overall organization of plant-pollinator interactions. We calculated network specialization ($H_2$' index[76]), which estimates the degree of niche partitioning or complementary resource use in the network [78]. We also calculated network nestedness (weighted NODF index[79]), which describes the degree to which specialist species within networks interact with generalists' interaction partners. Both network-level metrics were calculated with *networklevel* in *bipartite*. Together these species- and network-level metrics (Figure 3B-F) describe the variety, intensity, and specialization of pollinator visitation to plants' flowers and the properties of plant-pollinator associations at the level of entire assemblages.

We assessed the impact of herbivore presence and rainfall site on plant-pollinator interaction patterns using a generalized linear mixed-effects model framework similar to that described above. We constructed four candidate models for each metric (treatment, site, treatment + site, treatment×site), each of which included random intercepts for experimental block (i.e., paired Exclusion and Open plots) nested in site. Because the number of pollinator species per plant species, visitation intensity, and pollinator specialization were all estimated for each species in each plot, we also included species-level random effects in candidate models for these metrics. We used *DHARMa* (v0.3.2[70]) to perform residual diagnostics. We used a negative binomial error distribution for models of the number of pollinator species per plant species to account for overdispersion, Beta error distributions for network specialization to account for its unit interval (after transforming in accordance with [80]), and Gaussian error distributions for visitation intensity, pollinator specialization, and nestedness. Visitation intensity was log-transformed to fit distributional assumptions. We used a Gaussian error distribution for pollinator specialization, despite its unit interval bounds, in lieu of a Beta error distribution based on the residual diagnostics for both. To assess how herbivore presence and site influenced plant-pollinator interaction patterns, we compared candidate models with and without each variable using likelihood-ratio tests with the *anova* function in R. To parse the degree to which the effects of herbivory and site on plant-pollinator network structure were mediated by changes in the richness and abundance of the plant and pollinator assemblages, we performed a second set of likelihood-ratio tests for network specialization and nestedness. We compared candidate models including either herbivore presence or site as well as the richness of the network and total number of scaled interactions per plot (a proxy for combined plant and pollinator abundance) against a simpler model including only richness and scaled interactions.

***Pollinator Extinction Risk Estimation*:** To relate the effects of herbivore presence and site to plant-pollinator assemblage stability, we estimated the number of pollinators from each network expected to be lost to extinction based on their abundance and interaction patterns. To do this, we used a Bayesian network approach[41,40] to estimate pollinator loss. Briefly, this approach involves first estimating each pollinator's vulnerability to extinction based on its abundance (i.e., prior extinction probability[41]) and then using Bayesian networks with a linear relationship between posterior extinction risk and interaction partner loss (i.e., extinction risk increases linearly as interaction partners are lost) to estimate each pollinator's additional risk of extinction arising from their interaction patterns (i.e., posterior extinction risk that accounts for abundance and interactions). This Bayesian approach builds on previous approaches to extinction simulations by effectively averaging across all possible extinction scenarios[40] rather than using a small sample of simulation space. To generate extinction priors for each of the species in each network, floral abundance and pollinators caught were totaled at the site-by-treatment level to describe each plant and pollinator species' abundance in each combination of herbivory and rainfall scenarios. These values were then linearized and transformed into prior extinction probabilities following the approach in[41] at which point they represent each species' vulnerability to extinction based on their abundance. The extinction vulnerability of each pollinator attributed to both their abundance and interaction patterns was represented by the posterior extinction risk attributed to each species. The expected pollinator loss from each network was the sum of the posterior pollinator-extinction probabilities. Finally, to account for differing numbers of pollinators per network, we divided expected pollinator loss by the total number of pollinator species observed in each network. To assess whether expected proportional pollinator loss varied systematically with herbivore presence and site, we compared generalized linear mixed-effects models (beta error distribution) by likelihood-ratio test (Figure 3G). As above, four candidate models were constructed (treatment, site, treatment + site, treatment×site), each with a random intercept for block (nested in site). As with network structural metrics, we also assessed the degree to which richness and abundance drive herbivore and aridity effects on expected pollinator loss. We used likelihood-ratio tests to assess whether a full model containing herbivore treatment or site alongside network richness (log) and total scaled interactions (log) fit significantly better than simpler models where treatment or site, respectively, were not included.

## References:

1. Ollerton, J., Winfree, R., and Tarrant, S. (2011). How many flowering plants are pollinated by animals? Oikos *120*, 321–326.

2. Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., and Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. Proc. Biol. Sci. *274*, 303–313.

3. Bascompte, J., and Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. Annual Review of Ecology, Evolution, and Systematics *38*, 567–593.

4. Thébault, E., and Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. Science *329*, 853–856.

5. Daskin, J.H., Stalmans, M., and Pringle, R.M. (2016). Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. Journal of Ecology *104*, 79–89.

6. Holdo, R.M., Sinclair, A.R.E., Dobson, A.P., Metzger, K.L., Bolker, B.M., Ritchie, M.E., and Holt, R.D. (2009). A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. PLoS Biol. *7*, e1000210.

7. Pringle, R.M., Young, T.P., Rubenstein, D.I., and McCauley, D.J. (2007). Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. Proceedings of the National Academy of Sciences *104*, 193–197.

8. Olff, H., and Ritchie, M.E. (1998). Effects of herbivores on grassland plant diversity. Trends Ecol. Evol. *13*, 261–265.

9. Fleming, P.A., Hofmeyr, S.D., Nicolson, S.W., and du Toit, J.T. (2006). Are giraffes pollinators or flower predators of Acacia nigrescens in Kruger National Park, South Africa? Journal of Tropical Ecology *22*, 247–253.

10. Goheen, J.R., Palmer, T.M., Charles, G.K., Helgen, K.M., Kinyua, S.N., Maclean, J.E., Turner, B.L., Young, H.S., and Pringle, R.M. (2013). Piecewise disassembly of a large-herbivore community across a rainfall gradient: the UHURU experiment. PLoS One *8*, e55192.

11. Fornara, D.A., and Du Toit, J.T. (2007). Browsing lawns? Responses of Acacia nigrescens to ungulate browsing in an African savanna. Ecology *88*, 200–209.

12. Milchunas, D.G., and Lauenroth, W.K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments: Ecological archives M063-001. Ecol. Monogr. *63*, 327–366.

13. Bascompte, J., and Jordano, P. (2013). Mutualistic Networks.

14. Dunne, J.A., Williams, R.J., and Martinez, N.D. (2002). Food-web structure and network theory: The role of connectance and size. Proc. Natl. Acad. Sci. U. S. A. *99*, 12917–12922.

15. Pocock, M.J.O., Evans, D.M., and Memmott, J. (2012). The robustness and restoration of a network of ecological networks. Science *335*, 973–977.

16. Kaiser-Bunbury, C.N., Mougal, J., Whittington, A.E., Valentin, T., Gabriel, R., Olesen, J.M., and Blüthgen, N. (2017). Ecosystem restoration strengthens pollination network resilience and function. Nature *542*, 223–227.

17. Brosi, B.J., Niezgoda, K., and Briggs, H.M. (2017). Experimental species removals impact the architecture of pollination networks. Biol. Lett. *13*.

18. Ebeling, A., Klein, A.-M., and Tscharntke, T. (2011). Plant–flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. Basic and Applied Ecology *12*, 300–309.

19. Vanbergen, A.J., Espíndola, A., and Aizen, M.A. (2018). Risks to pollinators and pollination from invasive alien species. Nat Ecol Evol *2*, 16–25.

20. Lopezaraiza–Mikel, M.E., Hayes, R.B., Whalley, M.R., and Memmott, J. (2007). The impact of an alien plant on a native plant–pollinator network: an experimental approach. Ecology Letters *10*, 539–550.

21. Vázquez, D.P., and Simberloff, D. (2004). Indirect effects of an introduced ungulate on pollination and plant reproduction. Ecological Monographs *74*, 281–308.

22. Gillespie, S.D., and Adler, L.S. (2013). Indirect effects on mutualisms: parasitism of bumble bees and pollination service to plants. Ecology *94*, 454–464.

23. Tylianakis, J.M., and Morris, R.J. (2017). Ecological Networks Across Environmental Gradients. Annual Review of Ecology, Evolution, and Systematics *48*, 25–48.

24. Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Scott Mills, L., Daily, G., Castilla, J.C., Lubchenco, J., and Paine, R.T. (1996). Challenges in the Quest for Keystones. BioScience *46*, 609–620.

25. Prins, H.H.T., and van der Jeugd, H.P. (1993). Herbivore Population Crashes and Woodland Structure in East Africa. Journal of Ecology *81*, 305.

26. Coverdale, T.C., Kartzinel, T.R., Grabowski, K.L., Shriver, R.K., Hassan, A.A., Goheen, J.R., Palmer, T.M., and Pringle, R.M. (2016). Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. Ecology *97*, 3219–3230.

27. Wigley, B.J., Fritz, H., Coetsee, C., and Bond, W.J. (2014). Herbivores shape woody plant communities in the Kruger National Park: Lessons from three long-term exclosures. Koedoe *56*.

28. Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., and Collen, B. (2014). Defaunation in the Anthropocene. Science *345*, 401–406.

29. Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., et al. (2015). Collapse of the world's largest herbivores. Sci Adv *1*, e1400103.

30. Daskin, J.H., and Pringle, R.M. (2018). Warfare and wildlife declines in Africa's protected areas. Nature *553*, 328–332.

31. Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. Science *199*, 1302–1310.

32. Paine, R.T. (1966). Food Web Complexity and Species Diversity. American Naturalist *100*, 65–75.

33. Rohr, R.P., Saavedra, S., and Bascompte, J. (2014). Ecological networks. On the structural stability of mutualistic systems. Science *345*, 1253497.

34. Vanbergen, A.J., Woodcock, B.A., Heard, M.S., and Chapman, D.S. (2017). Network size, structure and mutualism dependence affect the propensity for plant–pollinator extinction cascades. Funct. Ecol. *31*, 1285–1293.

35. Oleques, S.S., Vizentin-Bugoni, J., and Overbeck, G.E. (2019). Influence of grazing intensity on patterns and structuring processes in plant--pollinator networks in a subtropical grassland. Arthropod Plant Interact. *13*, 757–770.

36. Rodriguez-Cabal, M.A., Barrios-Garcia, M.N., Amico, G.C., Aizen, M.A., and Sanders, N.J. (2013). Node-by-node disassembly of a mutualistic interaction web driven by species introductions. Proc. Natl. Acad. Sci. U. S. A. *110*, 16503–16507.

37. Augustine, D.J. (2010). Response of native ungulates to drought in semi-arid Kenyan rangeland: Ungulate response to drought. Afr. J. Ecol. *48*, 1009–1020.

38. Coe, M.J., Cumming, D.H., and Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. Oecologia *22*, 341–354.

39. Chao, A., and Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology *93*, 2533–2547.

40. Eklöf, A., Tang, S., and Allesina, S. (2013). Secondary extinctions in food webs: a Bayesian network approach. Methods in Ecology and Evolution *4*, 760–770.

41. Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Morse, H., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., et al. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. Nat Ecol Evol *3*, 363–373.

42. Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G., and Knops, J.M.H. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecol. Lett. *9*, 780–788.

43. Herrero, M., Ringler, C., van der Steeg, J., Thornton, P., Zhu, T., Bryan, E., Omolo, A., Koo, J., and Notenbaert, A. (2010). Climate variability and climate change and their impacts on Kenya's agricultural sector (International Livestock Research Institute).

44. Veldhuis, M.P., Ritchie, M.E., Ogutu, J.O., Morrison, T.A., Beale, C.M., Estes, A.B., Mwakilema, W., Ojwang, G.O., Parr, C.L., Probert, J., et al. (2019). Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. Science *363*, 1424–1428.

45. Ogutu, J.O., Piepho, H.-P., Said, M.Y., Ojwang, G.O., Njino, L.W., Kifugo, S.C., and Wargute, P.W. (2016). Extreme Wildlife Declines and Concurrent Increase in Livestock Numbers in Kenya: What Are the Causes? PLoS One *11*, e0163249.

46. Goheen, J.R., Augustine, D.J., Veblen, K.E., Kimuyu, D.M., Palmer, T.M., Porensky, L.M., Pringle, R.M., Ratnam, J., Riginos, C., Sankaran, M., et al. (2018). Conservation lessons from large-mammal manipulations in East African savannas: the KLEE, UHURU, and GLADE experiments. Ann. N. Y. Acad. Sci. *1429*, 31–49.

47. Louthan, A., Valencia, E., Martins, D.J., Guy, T., Goheen, J., Palmer, T., and Doak, D. (2019). Large mammals generate both top-down effects and extended trophic cascades on floral-visitor assemblages. Journal of Tropical Ecology *35*, 185–198.

48. Sinclair, A.R.E. (1979). The Eruption of the Ruminants. In Serengeti: Dynamics of an Ecosystem, A. R. E. Sinclair and M. Norton-Griffiths, eds. (University of Chicago Press), pp. 82–103.

49. Wigley, B.J., Augustine, D.J., Coetsee, C., Ratnam, J., and Sankaran, M. (2020). Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna. Ecology *101*, e03008.

50. Sinclair, A.R.E., Metzger, K., Brashares, J.S., Nkwabi, A., Sharam, G., and Fryxell, J.M. (2010). Trophic cascades in African savanna: Serengeti as a case study. Trophic cascades: predators, prey and the changing dynamics of nature *20*, 255–274.

51. Waldram, M.S., Bond, W.J., and Stock, W.D. (2008). Ecological engineering by a mega-grazer: White rhino impacts on a south African Savanna. Ecosystems *11*, 101–112.

52. Ponisio, L.C., Wilkin, K., M'Gonigle, L.K., Kulhanek, K., Cook, L., Thorp, R., Griswold, T., and Kremen, C. (2016). Pyrodiversity begets plant-pollinator community diversity. Glob. Chang. Biol. *22*, 1794–1808.

53. Adedoja, O., Dormann, C.F., Kehinde, T., and Samways, M.J. (2019). Refuges from fire maintain pollinator-plant interaction networks. Ecol. Evol. *9*, 5777–5786.

54. Carbone, L.M., Tavella, J., Pausas, J.G., and Aguilar, R. (2019). A global synthesis of fire

effects on pollinators. Glob. Ecol. Biogeogr. *28*, 1487–1498.

55. Kartzinel, T.R., Chen, P.A., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L., Rubenstein, D.I., Wang, W., and Pringle, R.M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proc. Natl. Acad. Sci. U. S. A. *112*, 8019–8024.

56. Pringle, R.M., Prior, K.M., Palmer, T.M., Young, T.P., and Goheen, J.R. (2016). Large herbivores promote habitat specialization and beta diversity of African savanna trees. Ecology *97*, 2640–2657.

57. Ford, A.T., Goheen, J.R., Otieno, T.O., Bidner, L., Isbell, L.A., Palmer, T.M., Ward, D., Woodroffe, R., and Pringle, R.M. (2014). Large carnivores make savanna tree communities less thorny. Science *346*, 346–349.

58. Kihwele, E.S., Mchomvu, V., Owen- Smith, N., Hetem, R.S., Hutchinson, M.C., Potter, A.B., Olff, H., and Veldhuis, M.P. (2020). Quantifying water requirements of African ungulates through a combination of functional traits. Ecol. Monogr. *90*.

59. Atkins, J.L., Long, R.A., Pansu, J., Daskin, J.H., Potter, A.B., Stalmans, M.E., Tarnita, C.E., and Pringle, R.M. (2019). Cascading impacts of large-carnivore extirpation in an African ecosystem. Science *364*, 173–177.

60. le Roux, E., van Veenhuisen, L.S., Kerley, G.I.H., and Cromsigt, J.P.G.M. (2020). Animal body size distribution influences the ratios of nutrients supplied to plants. Proc. Natl. Acad. Sci. U. S. A. *117*, 22256–22263.

61. Gotelli, N.J., and Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters *4*, 379–391.

62. Blundell, M. (1987). Collins Guide to the Wild Flowers of East Africa (Harpercollins Pub Limited).

63. Gill, B.A., Musili, P.M., Kurukura, S., Hassan, A.A., Goheen, J.R., John Kress, W., Kuzmina, M., Pringle, R.M., and Kartzinel, T.R. (2019). Plant DNA- barcode library and community phylogeny for a semi- arid East African savanna. Molecular Ecology Resources *19*, 838–846.

64. Baldock, K.C.R., Memmott, J., Ruiz-Guajardo, J.C., Roze, D., and Stone, G.N. (2011). Daily temporal structure in African savanna flower visitation networks and consequences for network sampling. Ecology *92*, 687–698.

65. Beattie, A.J., and Hughes, L. (2002). Ant-plant interactions. In Plant-animal interactions: an evolutionary approach, C. M. Herrera and O. Pellmyr, eds. (Wiley-Blackwell), pp. 211–236.

66. Core Development Team, R., and Others (2016). R: A language and environment for statistical computing.

67. Chao, A., Chiu, C.-H., and Jost, L. (2014). Unifying Species Diversity, Phylogenetic Diversity, Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers. Annual Review of Ecology, Evolution, and Systematics *45*, 297–324.

68. Hsieh, T.C., Ma, K.H., and Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity ( H ill numbers). Methods in Ecology and Evolution *7*, 1451–1456.

69. Brooks, M., Mollie, Brooks, E., Kristensen, K., Koen, J., Benthem, V., Magnusson, A., Casper, Berg, W., et al. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal *9*, 378.

70. Hartig, F. (2020). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models.

71. Lüdecke, D., Makowski, D., and Waggoner, P. (2020). performance: Assessment of regression models performance.

72. Baselga, A., and Orme, C.D.L. (2012). betapart: an R package for the study of beta diversity. Methods in Ecology and Evolution *3*, 808–812.

73. Schroeder, P.J., and Jenkins, D.G. (2018). How robust are popular beta diversity indices to sampling error? Ecosphere *9*, e02100.

74. Borcard, D., Gillet, F., and Legendre, P. (2018). Numerical Ecology with R (Springer Science & Business Media).

75. Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., et al. (2019). vegan: Community Ecology Package. R package version 2.5-6.

76. Blüthgen, N., Menzel, F., and Blüthgen, N. (2006). Measuring specialization in species interaction networks. BMC Ecol. *6*, 9.

77. Dormann, C.F., Frund, J., Bluthgen, N., and Gruber, B. (2009). Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. The Open Ecology Journal *2*, 7–24.

78. Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. Basic and Applied Ecology *11*, 185–195.

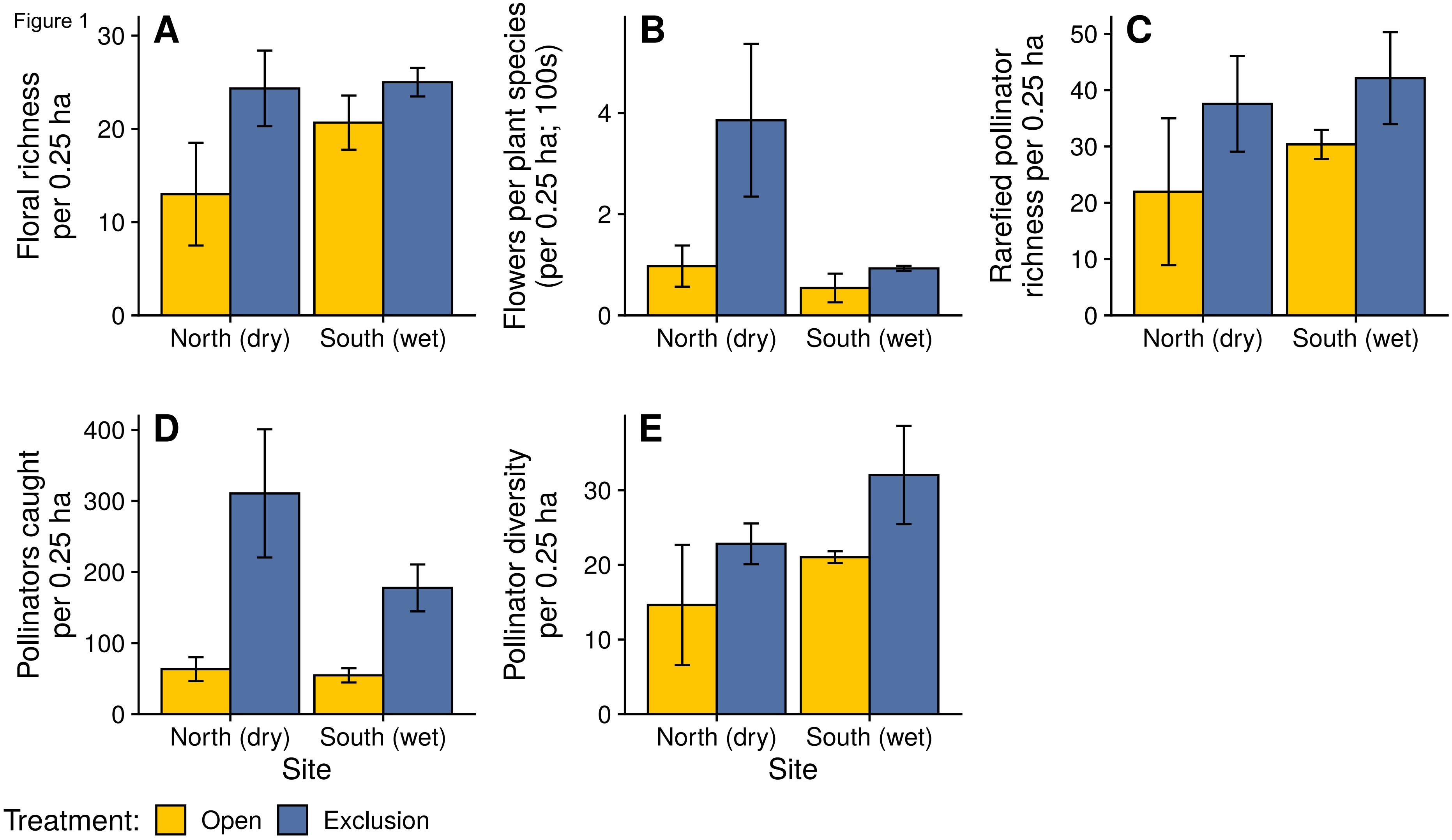
79. Almeida-Neto, M., and Ulrich, W. (2011). A straightforward computational approach for measuring nestedness using quantitative matrices. Environmental Modelling & Software *26*, 173–178.

80. Smithson, M., and Verkuilen, J. (2006). A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol. Methods *11*, 54–71.

## KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Biological Samples | | |
| Pollinator specimens collected | This paper | N/A |
| Deposited Data | | |
| Table of flowers counted | This paper | https://doi.org/10.5061/dryad.bcc2fqzc1 |
| Tables of pollinators caught with taxonomist-verified identities | This paper | https://doi.org/10.5061/dryad.bcc2fqzc1 |
| .Rdata file containing plant-pollinator interaction networks | This paper | https://doi.org/10.5061/dryad.bcc2fqzc1 |
| Software and Algorithms | | |
| R Statistical Software | R Project | https://www.r-project.org |
| Contributed R packages | Comprehensive R Archive Network (CRAN) | https://cran.r-project.org/ |
| Other | | |
| “UHURU” experiment | Mpala Research Center, Kenya | N/A |

Figure 1



A
Floral richness per 0.25 ha
0
10
20
30
B
Flowers per plant species (per 0.25 ha; 100s)
0
2
4
C
Rarefied pollinator richness per 0.25 ha
0
10
20
30
40
50
D
Pollinators caught per 0.25 ha
0
100
200
300
400
E
Pollinator diversity per 0.25 ha
0
10
20
30
North (dry)
South (wet)
Site
Treatment:
Open
Exclusion

Figure 2

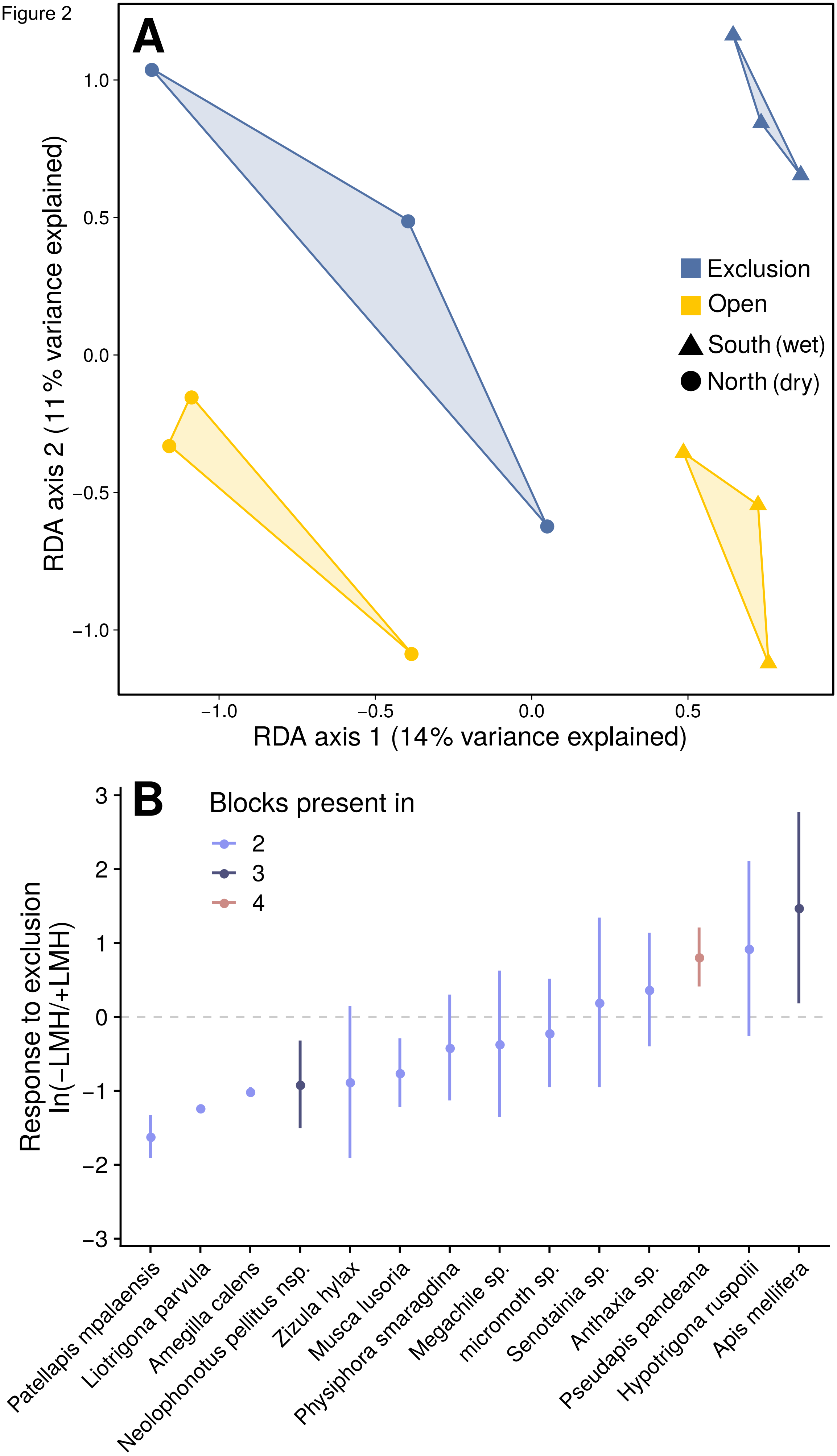
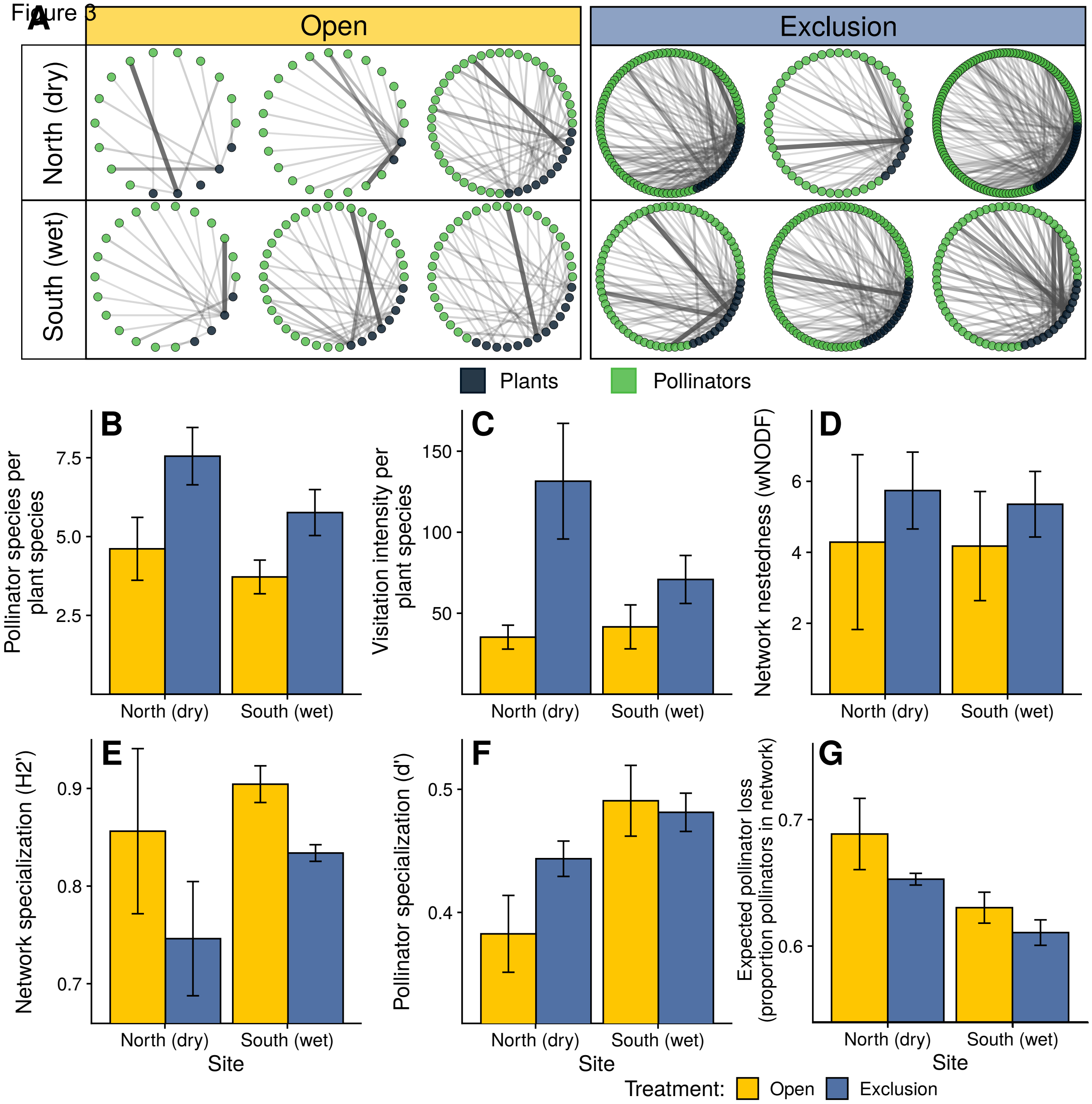

A
RDA axis 2 (11% variance explained)
1.0
0.5
0.0
−0.5
−1.0
RDA axis 1 (14% variance explained)
−1.0
−0.5
0.0
0.5
Exclusion
Open
South (wet)
North (dry)
B
Blocks present in
2
3
4
Response to exclusion
ln(−LMH/+LMH)
3
2
1
0
−1
−2
−3
Patellapis mpalaensis
Liotrigona parvula
Amegilla calens
Neolophonotus pellitus nsp.
Zizula hylax
Musca lusoria
Physiphora smaragdina
Megachile sp.
micromoth sp.
Senotainia sp.
Anthaxia sp.
Pseudapis pandeana
Hypotrigona ruspolii
Apis mellifera

Figure 3


A
Open
Exclusion
North (dry)
South (wet)
Plants
Pollinators
B
Pollinator species per plant species
7.5
5.0
2.5
North (dry)
South (wet)
C
Visitation intensity per plant species
150
100
50
North (dry)
South (wet)
D
Network nestedness (wNODF)
6
4
2
North (dry)
South (wet)
E
Network specialization (H2')
0.9
0.8
0.7
North (dry)
South (wet)
Site
F
Pollinator specialization (d')
0.5
0.4
North (dry)
South (wet)
Site
G
Expected pollinator loss (proportion pollinators in network)
0.7
0.6
North (dry)
South (wet)
Site
Treatment:
Open
Exclusion

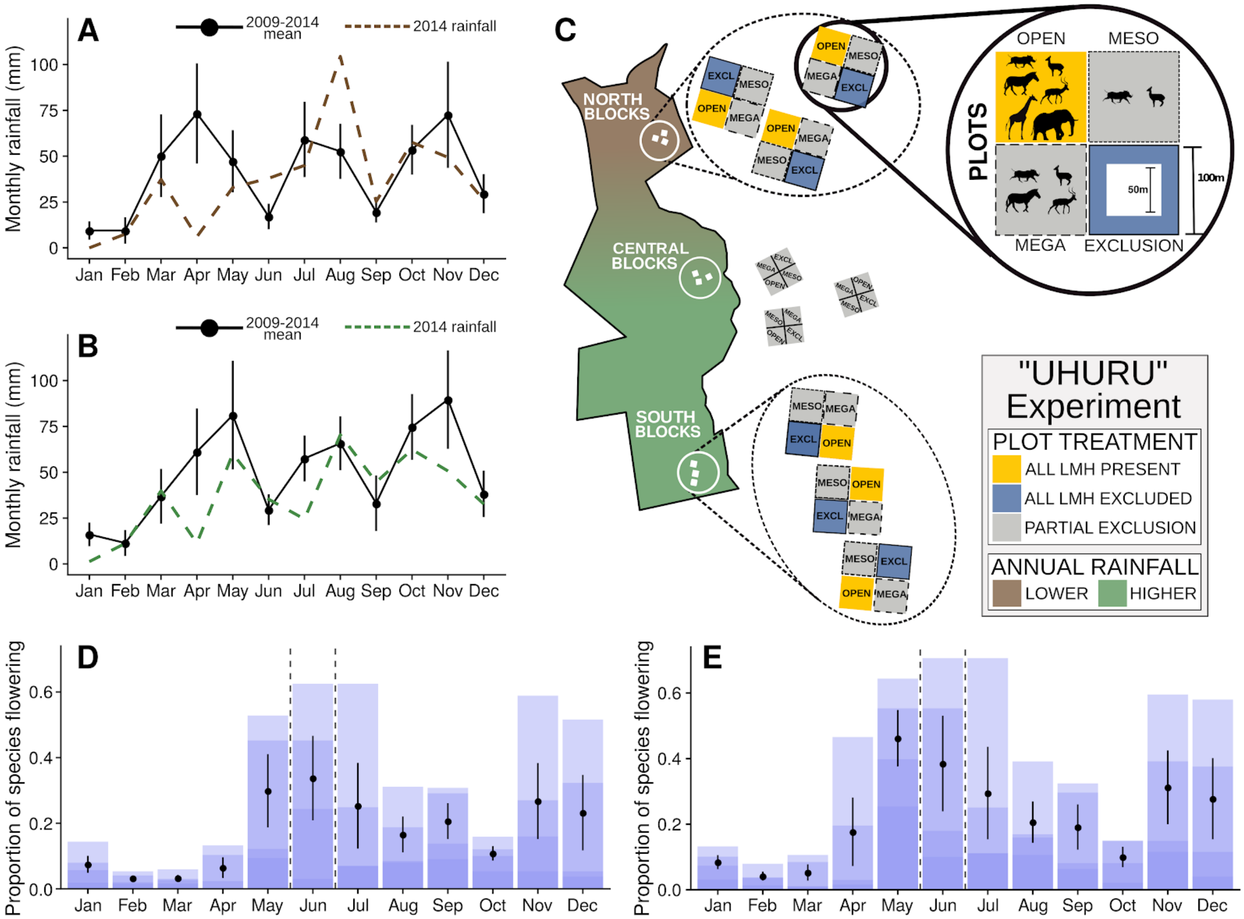


**Figure S1. Abiotic conditions and experimental setup, Related to STAR Methods.** The UHURU experiment at Mpala Conservancy (Laikipia, Kenya) consists of three experimental blocks at each of three sites arranged along a rainfall gradient (higher in the green, South; lower in the brown, North). (A-B) Average monthly rainfall (2009-2014) for North and South sites, respectively, is shown black lines (mean ± 1 SEM) and monthly rainfall for 2014 (when sampling was conducted) is shown by colored, dashed lines. (C) UHURU plots (100 x 100m; 1 ha) are located at three sites (North, Central, South) and each site contains three blocks of experimental treatments. Each block of the experiment contains four plots (100 x 100 m; 1 ha) that differ in treatment: total-exclusion (EXCLUSION; where all herbivores larger than 5 kg and 50 cm tall are excluded), meso-herbivore exclusion (MESO; excluding all herbivores larger than dik-dik, *Madoqua* cf. *guentheri* and warthog *Phacochoerus africanus*), mega-herbivore exclusion (MEGA; excluding just elephant, *Loxodonta africana*, and giraffe, *Giraffa camelopardalis*), and open (OPEN; where all herbivores have access) plots. The North and South sites, representing low- and high-rainfall respectively, were used in this experiment and are expanded in the figure. The Exclusion and Open plots that were sampled are shown in blue and yellow, respectively, whereas the plots not sampled (i.e., MESO and MEGA plots and all Central plots) are in grey. To ensure that our data reflected each treatment, we restricted our sampling of each 100 x 100 m (1 ha) plot to a 50 x 50m (0.25 ha) subplot located at the center of each plot, which is illustrated as the central, white square in the EXCLUSION plot of the expanded block (top right). To ensure complete sampling of each plot's central subplot, we split 50 x 50 m subplots into 25 quadrats of 10 x 10 m for sampling. (D-E) In addition, sampling was conducted during an annual peak in flowering. Bars show the proportion of plant species flowering each month across four years (2014-2015, 2017-2018) at the drier North site (D) and wetter South site (E). Each month in each year is represented by a semi-transparent bar such that the darkest areas indicate where the bars for all years overlap. Points and solid lines show the mean ± 1 SEM across the four years. Flowering showed two annual peaks that followed rainfall patterns closely (A-B); one from May-July and another in November-December. All data presented in Figures 1-3 were collected following the aforementioned use of the UHURU experiment and dashed vertical lines in D-E, above, indicate the timing of our sampling period (late May to early July).

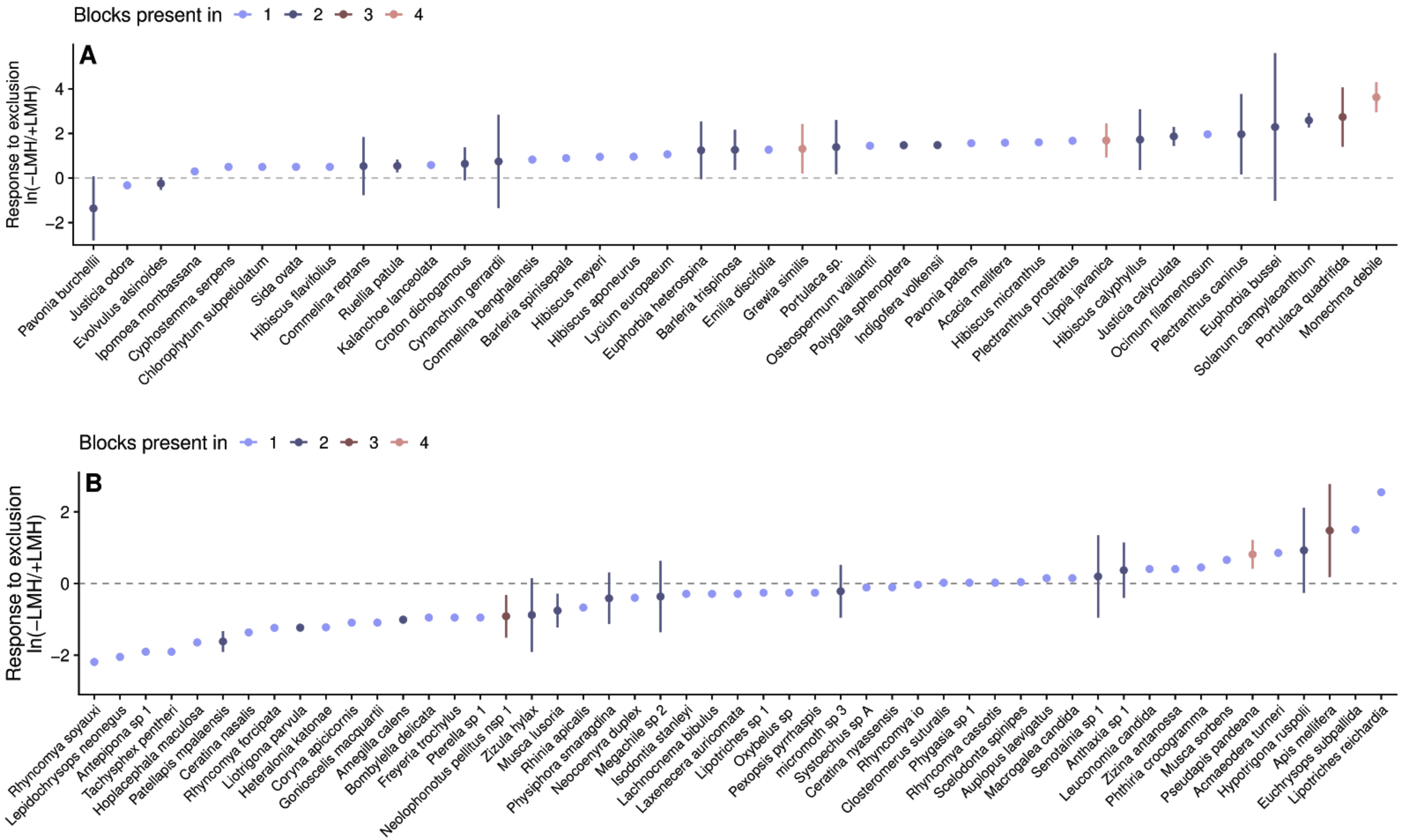

Blocks present in
1
2
3
4
A
Response to exclusion
ln(−LMH/+LMH)
4
2
0
−2
Pavonia burchellii
Justicia odora
Evolvulus alsinoides
Ipomoea mombassana
Cyphostemma serpens
Chlorophytum subpetiolatum
Sida ovata
Hibiscus flavifolius
Commelina reptans
Ruellia patula
Kalanchoe lanceolata
Croton dichogamous
Cynanchum gerrardii
Commelina benghalensis
Barleria spinisepala
Hibiscus meyeri
Hibiscus aponeurus
Lycium europaeum
Euphorbia heterospina
Barleria trispinosa
Emilia discifolia
Grewia similis
Portulaca sp.
Osteospermum vaillantii
Polygala sphenoptera
Indigofera volkensii
Pavonia patens
Acacia mellifera
Hibiscus micranthus
Plectranthus prostratus
Lippia javanica
Hibiscus calyphyllus
Justicia calyculata
Ocimum filamentosum
Plectranthus caninus
Euphorbia bussei
Solanum campylacanthum
Portulaca quadrifida
Monechma debile
Blocks present in
1
2
3
4
B
Response to exclusion
ln(−LMH/+LMH)
2
0
−2
Rhyncomya soyauxi
Lepidochrysops neonegus
Antepipona sp 1
Tachysphex pentheri
Hoplacephala maculosa
Patellapis mpalaensis
Ceratina nasalis
Rhyncomya forcipata
Liotrigona parvula
Heteraloina katonae
Coryna apicicornis
Gonioscelis macquartii
Amegilla calens
Bombylella delicata
Freyeria trochylus
Pterella sp 1
Neolophonotus pellitus nsp 1
Zizula hylax
Musca lusoria
Rhinia apicalis
Physiphora smaragdina
Neocoenyra duplex
Megachile sp 2
Isodontia stanleyi
Lachnocnema bibulus
Laxenecera auricomata
Lipotriches sp 1
Oxybelus sp
Pexopsis pyrrhaspis
micromoth sp 3
Systoechus sp A
Ceratina nyassensis
Rhynconya io
Closteromerus suturalis
Phygasia sp 1
Rhyncomya cassotis
Scelodonta spinipes
Auplopus laevigatus
Macrogalea candida
Senotainia sp 1
Anthaxia sp 1
Leuconomia candida
Zizina antanossa
Phthiria crocogramma
Musca sorbens
Pseudapis pandeana
Acmaeodera turneri
Hypotrigona ruspolii
Apis mellifera
Euchrysops subpallida
Lipotriches reichardia

**Figure S2. Species-specific responses to large herbivore exclusion, Related to Figures 1-2.** (A-B) As a complement to the analyses presented in Figure 1, we calculated the log-response ratio of floral and pollinator abundance (for plants, abundance was the number of flowers; for pollinators, it was the capture rate) in Exclusion plots (-LMH) compared to Open plots (+LMH) for all species that were observed in both plots of at least one block (pollinators captured in both plots of at least two blocks are shown in Figure 2). The y-axes show this response ratio for each species, with points colored by the number of experimental blocks a species was observed in (± 1 SEM when a species was present in both treatments of multiple blocks). (A) Of the 39 plant species for which a response ratio could be calculated, only three species had fewer flowers when large-herbivores were excluded (at left; negative response ratio). Across the 36 plant species that had more floral units when herbivores were excluded, the mean log-response ratio (± 1 SEM) was 1.33 ± 0.12, which translates to an almost fourfold increase in floral abundance per species on average when large herbivores are excluded. (B) A subset of pollinator species were captured at a higher rate when herbivores were excluded whereas others were captured at a lower rate. Pollinator responses to herbivore exclusion were calculated based on capture rate rather than capture frequencies to account for differences in total sampling time among plots. Species that have higher capture rates in Exclusion plots (positive response) tend to be foragers that specialize on nectar and pollen resources (e.g., *Apis*, *Lipotriches*, and *Hypotrigona* bees, *Euchrysops* and *Zizina* butterflies, *Acmaeodera* beetles, and *Phthiria* bee-flies) whereas species that have higher capture rates in Open plots (negative response to exclusion) were more trophically diverse and included predatory wasps (*Antepipona*, *Tachysphex*), predatory and detritivorous flies (*Gonioscelis*, *Hoplacephala*, *Pterella*, *Neolophonotus*), herbivorous beetles (*Coryna*) as well as nectar and pollen specialists (e.g., *Patellapis*, *Ceratina*, *Liotrigona* bees, *Lepidochrysops* and *Freyeria* butterflies, and *Heteralonia* and *Bombylella* bee-flies).

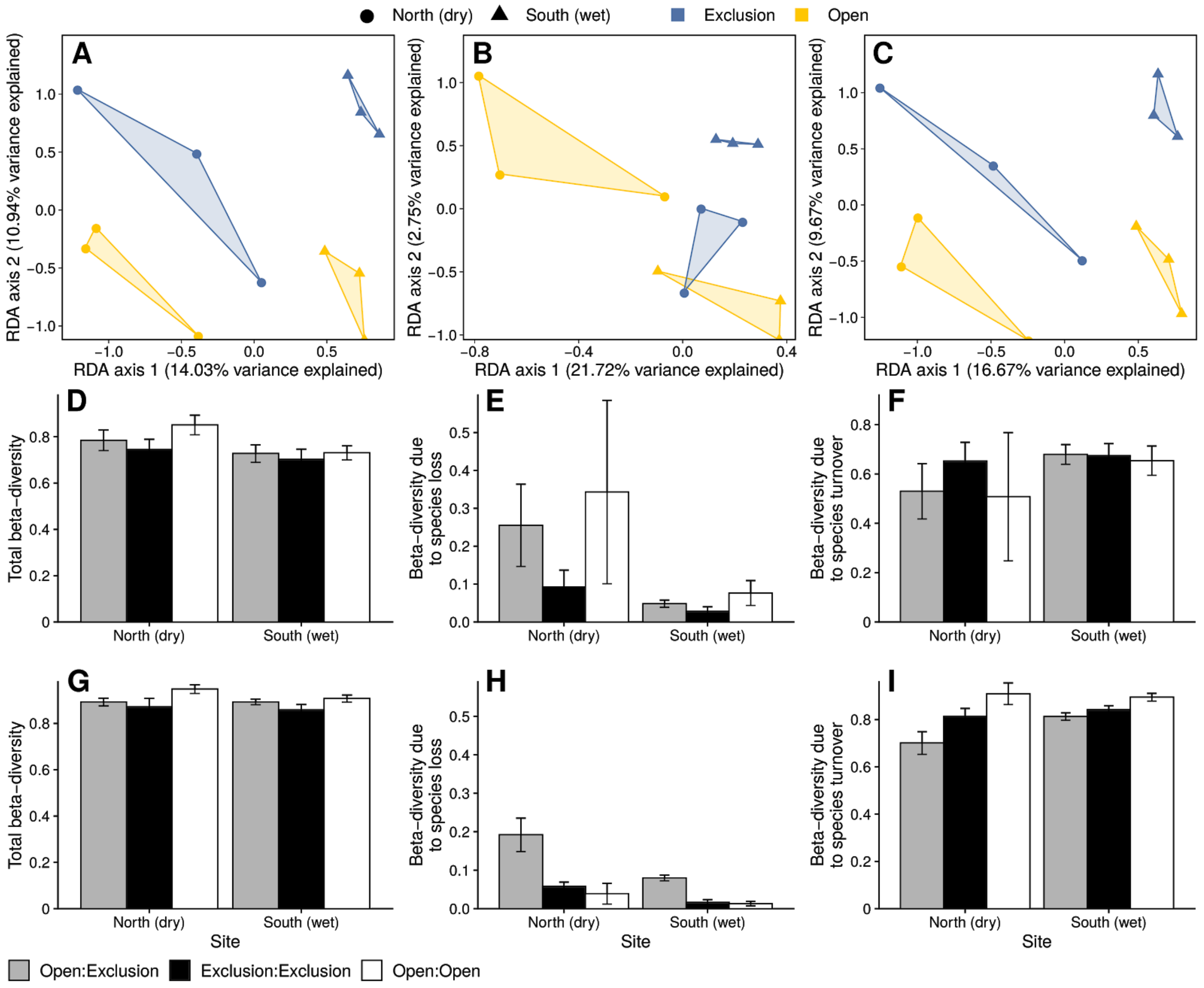


**Figure S3. Compositional dissimilarity in pollinator and floral assemblages, Related to Figure 2.** (A-C) Partial distance-based redundancy analyses of pollinator-assemblage dissimilarity components (A, total dissimilarity, is also shown in Figure 2). In each, circular points represent lower rainfall sites (North plots) and triangular points represent higher rainfall sites (South plots). Blue points show Exclusion plots and yellow points show Open plots. (A) Total pollinator dissimilarity ($\beta_{JAC}$) was driven by site (represented by x-axis) whereas herbivory treatment (represented by y-axis) had a lesser effect (permutational ANOVA, n = 9999, adjusted $R^2 = 0.06$; Site, $F_{1,8} = 1.48$, $P = 0.002$; Treatment, $F_{1,8} = 1.17$, $P = 0.14$). (B) Dissimilarity due to nestedness (i.e., species loss between plots; $\beta_{JNE}$) was not significantly associated with treatment or site (permutational ANOVA, n = 9999, adjusted $R^2 = 0.48$; Site, $F_{1,8} = 1.20$, $P = 0.34$; Treatment, $F_{1,8} = 0.75$, $P = 0.55$). (C) Dissimilarity due to species turnover ($\beta_{SIM}$) was significantly predicted by site (x-axis) but not treatment (permutational ANOVA, $n = 9999$, adjusted $R^2 = 0.09$; Site, $F_{1,8} = 1.80$, $P < 0.001$; Treatment, $F_{1,8} = 1.09$, $P = 0.33$) though some separation by treatment is graphically apparent. (D-I) Compositional dissimilarity values for the floral assemblage (D-F) and pollinator assemblage (G-I) are displayed for the same three components: total dissimilarity (D, G), dissimilarity due to nestedness, or loss of species from one assemblage to the next (E, H), and dissimilarity due to turnover of species (F, I). Between-plot comparisons are grouped by treatment (Open-Exclusion comparisons, grey; Exclusion-Exclusion comparisons, black; Open-Open comparisons, white). For both floral (D) and pollinator (G) assemblages, total dissimilarity was lowest between Exclusion plots and tended to peak between Open plots. Dissimilarity resulting from nestedness was greatest between Open plots for flowers (E) whereas for pollinators, Open:Exclusion plot comparisons were higher (H), which may be suggestive of a filtering effect of large-mammalian herbivores on pollinator assemblages. In all cases, dissimilarity was dominated by the component attributed to species turnover (y-axis values greater in F and I compared to E and H) but did not differ consistently based on plot comparison for floral assemblages (F). For pollinators (I), Open plots tended to show greater dissimilarity due to species turnover suggesting that these assemblages may be more heterogeneous.

| Taxonomic Group | Taxonomist | Affiliation |
|---|---|---|
| Apidae | Eardley, Connal | Agricultural Resource Council, Pretoria, South Africa |
| Apoidea | Gikungu, Mary; Macharia, Jane | National Museums of Kenya, Nairobi, Kenya |
| Asilidae | Dikow, Torsten; Londt, Jason | National Museum of Natural History, Smithsonian Institution, Washington, USA; KwaZulu-Natal Museum, Pietermaritzburg, South Africa |
| Bombyliidae | Evenhuis, Neal | Bishop Museum, Honolulu, USA |
| Braconidae | Quicke, Donald | Chulalongkom University, Bangkok, Thailand |
| Calliphoridae | Deeming, John | National Museum Wales, Cardiff, UK |
| Chrysididae | Rosa, Paolo | Bernareggio, Italy |
| Coleoptera | Njoroge, Laban | National Museums of Kenya, Nairobi, Kenya |
| Formicidae | Martins, Dino | Mpala Research Center, Laikipia, Kenya |
| Gasteruptiidae | van Noort, Simon | Iziko Museums of South Africa, Cape Town, South Africa |
| Halictidae | Pauly, Alain | Royal Belgian Institute of Natural Sciences, Brussels, Belgium |
| Hemiptera | Halbert, Susan | Florida Department of Agriculture, Gainesville, USA |
| Lepidoptera | Hayden, James; Mugambi, Joseph; Warren, Andy | Florida Department of Agriculture, Gainesville, USA; National Museums of Kenya, Nairobi, Kenya; Florida Museum of Natural History, Gainesville, USA |
| Megachilidae | Eardley, Connal | Agricultural Resource Council, Pretoria, South Africa |
| Muscidae | Deeming, John; Pont, Adrian | National Museum Wales, Cardiff, USA; Oxford University Museum of Natural History, Oxford, UK |
| Pompilidae | Wahis, Raymond | Universite de Liege, Gembloux, Belgium |
| Sarcophagidae | Whitmore, Daniel | Natural History Museum, London, UK |
| Scolidae | Schulten, Gerard | Naturalis Biodiversity Center, Leiden, Netherlands |
| Sphecidae | Pulawski, Wojciech | California Academy of Sciences, San Francisco, USA |
| Syrphidae | Whittington, Andrew | Bournemouth University, Poole, UK |
| Tachinidae | Cerretti, Pierfilippo | University of Padova, Padova, Italy |

| | | |
|---|---|---|
| Tephritidae | Steck, Gary | Florida Department of Agriculture, Gainesville, USA |
| Vespidae | Carpenter, James; Williams, Kevin | American Museum of Natural History, New York, USA; Florida Department of Agriculture, Gainesville, USA |

**Table S1. Taxonomic experts responsible for specimen sorting and identification, Related to STAR Methods.** Taxonomic experts who assisted in either (i) initial sorting of specimens to taxonomic family (i.e., those associated with higher taxonomic groups in the table), or (ii) identified captured specimens to the lowest possible taxonomic level. Specimens are deposited in home institutions of each taxonomist.

| **Variable** | **Full** | **Null** | **Family** | **DF F** | **DF N** | **$\chi^2$** | ***P*-value** |
|---|---|---|---|---|---|---|---|
| Floral richness | **Plot treatment**, site, site:block (RE) | Site, site:block (RE) | genpois(link = ‘log’) | 5 | 4 | 5.64 | 0.02 |
| Floral richness | Plot treatment, **site**, site:block (RE) | Plot treatment, site:block (RE) | genpois(link = ‘log’) | 5 | 4 | 0.98 | 0.32 |
| Floral richness | **Plot treatment * site**, site:block (RE) | Plot treatment, site, site:block (RE) | genpois(link = ‘log’) | 6 | 5 | 3.10 | 0.08 |
| Flowers per plant species (log) | **Plot treatment**, site, site:block (RE) | Site, site:block (RE) | gaussian(link = ‘identity’) | 5 | 4 | 9.68 | 0.002 |
| Flowers per plant species (log) | Plot treatment, **site**, site:block (RE) | Plot treatment, site:block (RE) | gaussian(link = ‘identity’) | 5 | 4 | 2.40 | 0.12 |
| Flowers per plant species (log) | **Plot treatment * site**, site:block (RE) | Plot treatment, site, site:block (RE) | gaussian(link = ‘identity’) | 6 | 5 | 1.88 | 0.17 |
| Rarefied pollinator richness | **Plot treatment**, site, site:block (RE) | Site, site:block (RE) | gaussian(link = ‘identity’) | 5 | 4 | 5.10 | 0.02 |
| Rarefied pollinator richness | Plot treatment, **site**, site:block (RE) | Plot treatment, site:block (RE) | gaussian(link = ‘identity’) | 5 | 4 | 0.49 | 0.48 |
| Rarefied pollinator richness | **Plot treatment * site**, site:block (RE) | Plot treatment, site, site:block (RE) | gaussian(link = ‘identity’) | 6 | 5 | 0.16 | 0.69 |
| Pollinators caught | **Plot treatment**, site, log(effort), site:block (RE) | Site, log(effort), site:block (RE) | genpois(link = ‘log’) | 6 | 5 | 3.94 | 0.05 |
| Pollinators caught | Plot treatment, **site**, log(effort), site:block (RE) | Plot treatment, log(effort), site:block (RE) | genpois(link = ‘log’) | 6 | 5 | 0.02 | 0.88 |
| Pollinators caught | **Plot treatment * site**, log(effort), site:block (RE) | Plot treatment, site, log(effort), site:block (RE) | genpois(link = ‘log’) | 7 | 6 | 1.33 | 0.25 |
| Pollinator diversity | **Plot treatment,** site, site:block (RE) | Site, site:block (RE) | gaussian(link = ‘identity’) | 5 | 4 | 4.51 | 0.03 |
| Pollinator diversity | Plot treatment, **site**, site:block (RE) | Plot treatment, site:block (RE) | gaussian(link = ‘identity’) | 5 | 4 | 2.03 | 0.15 |
| Pollinator diversity | **Plot treatment * site**, site:block (RE) | Plot treatment, site, site:block (RE) | gaussian(link = ‘identity’) | 6 | 5 | 0.14 | 0.70 |
| Pollinator species caught per plant species | **Plot treatment,** site, site:block (RE), plant species (RE) | Site, site:block (RE), plant species (RE) | nbinom1(link - ‘log’) | 6 | 5 | 9.31 | 0.002 |
| Pollinator species caught per plant species | Plot treatment, **site**, site:block (RE), plant species (RE) | Plot treatment, site:block (RE), plant species (RE) | nbinom1(link - ‘log’) | 6 | 5 | 3.47 | 0.06 |
| Pollinator species caught per plant species | **Plot treatment * site**, site:block (RE), plant species (RE) | Plot treatment, site, site:block (RE), plant species (RE) | nbinom1(link - ‘log’) | 7 | 6 | 0.43 | 0.51 |
| Visitation intensity (log) | **Plot treatment**, site, site:block (RE), plant species (RE) | Site, site:block (RE), plant species (RE) | gaussian(link = ‘identity’) | 6 | 5 | 5.66 | 0.02 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Visitation intensity (log) | Plot treatment, **site**, site:block (RE), plant species (RE) | Plot treatment, site:block (RE), plant species (RE) | gaussian(link = ‘identity’) | 6 | 5 | 0.56 | 0.46 |
| Visitation intensity (log) | **Plot treatment * site**, site:block (RE), plant species (RE) | Plot treatment, site, site:block (RE), plant species (RE) | gaussian(link = ‘identity’) | 7 | 6 | 1.19 | 0.28 |
| Pollinator specialization | **Plot treatment**, site, site:block (RE), pollinator species (RE) | Site, site:block (RE), pollinator species (RE) | gaussian(link = ‘identity’) | 6 | 5 | 0.69 | 0.41 |
| Pollinator specialization | Plot treatment, **site**, site:block (RE), pollinator species (RE) | Plot treatment, site:block (RE), pollinator species (RE) | gaussian(link = ‘identity’) | 6 | 5 | 1.20 | 0.27 |
| Pollinator specialization | **Plot treatment * site**, site:block (RE), pollinator species (RE) | Plot treatment, site, site:block (RE), pollinator species (RE) | gaussian(link = ‘identity’) | 7 | 6 | 1.35 | 0.24 |
| Nestedness | **Plot treatment**, site, site:block (RE) | Site, site:block (RE) | gaussian(link = ‘identity’) | 5 | 4 | 1.34 | 0.25 |
| Nestedness | Plot treatment, **site**, site:block (RE) | Plot treatment, site:block (RE) | gaussian(link = ‘identity’) | 5 | 4 | 0.03 | 0.87 |
| Nestedness | **Plot treatment * site**, site:block (RE) | Plot treatment, site, site:block (RE) | gaussian(link = ‘identity’) | 6 | 5 | 0.02 | 0.90 |
| Nestedness | **Plot treatment**, network richness (log), total interactions (log) | Network richness (log), total interactions (log) | gaussian(link = ‘identity’) | 5 | 4 | 1.68 | 0.20 |
| Nestedness | **Site**, network richness (log), total interactions (log) | Network richness (log), total interactions (log) | gaussian(link = ‘log’) | 5 | 4 | 0.04 | 0.85 |
| Network specialization | **Plot treatment**, site, site:block (RE) | Site, site:block (RE) | beta_family(link = ‘logit’) | 5 | 4 | 4.43 | 0.04 |
| Network specialization | Plot treatment, **site**, site:block (RE) | Plot treatment, site:block (RE) | beta_family(link = ‘logit’) | 5 | 4 | 0.90 | 0.34 |
| Network specialization | **Plot treatment * site**, site:block (RE) | Plot treatment, site, site:block (RE) | beta_family(link = ‘logit’) | 6 | 5 | 0.36 | 0.55 |
| Network specialization | **Plot treatment**, network richness (log), total interactions (log) | Network richness (log), total interactions (log) | beta_family(link = ‘logit’) | 5 | 4 | 0.07 | 0.80 |
| Network specialization | **Site**, network richness (log), total interactions (log) | Network richness (log), total interactions (log) | beta_family(link = ‘logit’) | 5 | 4 | 1.56 | 0.21 |
| Expected pollinator loss (proportion all pollinators in network) | **Plot treatment**, site, site:block (RE) | Site, site:block (RE) | beta_family(link = ‘logit’) | 5 | 4 | 3.60 | 0.06 |
| Expected pollinator loss (proportion all pollinators in network) | Plot treatment, **site**, site:block (RE) | Plot treatment, site:block (RE) | beta_family(link = ‘logit’) | 5 | 4 | 7.35 | 0.007 |
| Expected pollinator loss (proportion all pollinators in network) | **Plot treatment * site**, site:block (RE) | Plot treatment, site, site:block (RE) | beta_family(link = ‘logit’) | 6 | 5 | 0.49 | 0.49 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Expected pollinator loss (proportion all pollinators in network) | **Plot treatment**, network richness (log), total interactions (log) | Network richness (log), total interactions (log) | beta_family(link = ‘logit’) | 5 | 4 | 0.06 | 0.81 |
| Expected pollinator loss (proportion all pollinators in network) | **Site**, network richness (log), total interactions (log) | Network richness (log), total interactions (log) | beta_family(link = ‘logit’) | 5 | 4 | 9.40 | 0.002 |

**Table S2. Statistical model structure and fitting, Related to Figures 1-3, STAR Methods.** Statistical significance was assessed based on the comparison of the goodness-of-fit between a full model that contained a variable of interest and a null model that only contained other potentially explanatory variables. Full models and null models were fit with the *glmmTMB* function and package in R v0.2.3[S1] and compared using a likelihood-ratio test. ‘Variable’ refers to the dependent variable of the models. ‘Full’ and ‘Null’ refer to the composition of the full model and null model, respectively, and specify the fixed and random effects in the model with the variable of interest in bold. (RE) denotes a random effect and * denotes an interaction term. ‘Family’ is the error distribution implemented in each generalized linear mixed-effects model. ‘DF F’ and ‘DF N’ report the degrees of freedom for the full and null model, respectively. ‘$\chi^2$’ reports the chi-square statistic for the comparison of full and null model goodness-of-fit. ‘*P*-value’ reports the statistical significance of the comparison of model fit between the full model (i.e., containing the variable of interest) and the null model.

## Supplemental Reference

S1 Brooks, M., Mollie, Brooks, E., Kristensen, K., Koen, J., Benthem, V., Magnusson, A., Casper, Berg, W., et al. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal *9*, 378.